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Research report

The concept of brain plasticity—Paillard's systemic analysis and emphasis on structure and function (followed by the translation of a seminal paper by Paillard on plasticity)

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Abstract

Although rejected for the most part of the 20th Century, the idea of brain plasticity began to receive wide acceptance from the 1970s. Yet there has been relatively little theoretical comment on the definition and use of "plasticity" in the field of neurobiology. An early exception to this lack of critical reflection on neural plasticity was provided by Jacques Paillard in a seminal paper that he published in 1976 [Paillard J. Réflexions sur l'usage du concept de plasticité en neurobiology. J Psychol 1976;1:33–47]. As this valuable contribution was published in French, the present authors provide an English adaptation to help convey his ideas to an international audience, together with a contemporary commentary on this paper. Paillard's definition of the term "plasticity" is probably as pertinent today as it was 30 years ago, especially in terms of its relevance to multiple levels of analysis of brain function (molecular, cellular, systemic). Sadly, Jacques Paillard died in 2006; our comments therefore also include a brief biographical tribute to this outstanding neuroscientist.

Keywords: Brain; Concept; Elasticity; Flexibility; Function; Nervous system; Structure

1. Introduction

The principle of brain plasticity is readily acknowledged in contemporary neuroscience, but its general acceptance is relatively recent, beginning in the 1970s. Notions of neuroplasticity had certainly existed previously (e.g., [5]), but the broad concept became current only after the early findings on enriched environments (e.g., [36]) and visual deprivation (e.g., [18]) had been established. Resistance against the principle of brain plasticity was probably mainly due to the influence of the great Spanish neuroanatomist, Santiago Ramon y Cajal, who had firmly postulated that neural connections in the adult brain are fixed and immutable [35]. From this perspective, it is intriguing that Ramon y Cajal himself had speculated that mental exercise, such as learning a musical instrument, might be associated with an increase in the growth of new axon collaterals and new terminal dendrites [34]. This conjecture, which was made prior to the use of the word "synapse" by Sherrington in 1897, was a forerunner to the more recent speculation on "cell assemblies" [17]. Of course, previously neglected concepts of plasticity are universally endorsed in contemporary neuroscience (e.g., for plasticity of spinal neural circuitry [10]; for discussions of the functional properties of neurogenesis, see [2,14,21]. One challenge facing contemporary neuroscience is, however, the almost unbridled proliferation of examples of "brain plasticity". This apparently simple and attractive concept is instead an extraordinary complex and elusive issue, exacerbated by the fact that the idea is conveyed differently by different subdisciplines and often at multiple levels of analysis (from genetic to behavioural). This important issue was encapsulated by an early theoretical paper on this topic [31]. As many of the inherent problems with plasticity remain unanswered today, the current paper provides a contemporary perspective on Paillard's ideas, accompanied by an English translation of his original article. Many of Paillard's comments are perhaps as relevant today as they were at the original time of writing, because they challenge researchers

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to address the functional properties of any neural change. Sadly, Jacques Paillard died in July 2006. Partly in tribute to this outstanding behavioural neuroscientist, and partly in view of the importance of neural plasticity today, we hope that these contributions will be of value to the ongoing debate on brain plasticity.

Paillard's seminal paper was published only shortly after the first demonstration of long-term potentiation (LTP) in the mammalian hippocampus [6]. It sought to provide a meaningful definition of "change" that was sufficient to warrant the label (neuro-) "plasticity". Using systemic analysis as his conceptual framework [44], Paillard briefly covered this "new" concept from an elementary to a holistic level of analysis. Jacques Paillard's 1976 paper on neural plasticity [31] was perhaps one of his most significant, amongst a productivity that spanned 150 French and 143 English peer-reviewed articles. His last paper was published in 2006 [39] (see http://jacquespaillard.apinc.org/). Paillard's work covered a wide range of fundamental, psychological and medical issues. Many were reviews or conceptual papers that dealt with the plasticity in the central nervous system (CNS). The 1976 paper was published in the first issue of the *Journal de Psychologie*, and was entitled *"Réflexions sur l'usage du concept de plasticité en neurobiologie*" (Reflections on the use of the concept of plasticity in neurobiology). Given its relevance to CNS plasticity, the English translation of Paillard's 1976 paper will make it more readily available to a broader audience.

Jacques Paillard was born on 5th March 1920 in Nemours, 90 km south-east of Paris. His primary expertise was the neurophysiology of sensorimotor integration and the perception of body space. In 1947, he was recruited to the then relatively new *Centre National de la Recherche Scientifique* (CNRS) in Paris, which had been created in 1939, starting his research work in Alfred Fessard's[1] laboratory. Ten years later, he moved to the Faculty of Sciences in Marseille where he became a full-professor and one of the leading figures in psychophysiology and motor function in France, achieving an international reputation. Paillard is perhaps best known in France for establishing the CNRS Institute of Neurophysiology and Psychophysiology in Marseille in 1965, which provided an innovative model framework for research in cognitive neuroscience: brain functions were investigated at a variety of integrative levels, from cell function to fully integrated behaviour, using both human data and animal models. With Professor Larry Weiskrantz, Jacques Paillard co-founded the European Brain and Behaviour Society (EBBS), in 1968, and was part of an original council that included figures such as Elisabeth Warrington, Giovani Berlucchi, Konrad Ackert and Hans Kuypers. One year later, Paillard was the local organizer of the very first EBBS meeting. The EBBS still plays a major role in the field of behavioural neuroscience (its last meeting was in Triest, Italy, September 2007).

[1] Until the early 1970s, Alfred Fessard was the head of the *Institut Marey* in Paris. At present, there is an *Institut de Neurobiologie Alfred Fessard* in Gif-sur-Yvette, near Paris.

Paillard's definition of plasticity has the great advantage of clarifying a concept that has been used with different meanings by many people. According to Paillard ([31]; see translation at the end of this article), "The term plasticity is only appropriate in terms of the ability of a system to achieve novel functions, either by transforming its internal connectivity or by changing the elements of which it is made" (p. 43 in the French version; caption of Fig. 2). That is, if there is no new function or no structural change underlying this new function, then plasticity is not the appropriate term.

2. The nature of plastic changes: plasticity vs. flexibility

Using this definition, Paillard cautioned that not every change in the neural system is obligatorily plastic. That is, only those changes that are both structural and functional were defined as plastic changes. Functional adaptations based on preprogrammed or expected environmental changes in hard-wired systems, as in many robots, should not be considered examples of plasticity. As he pointed out in a companion paper, for robots, "each control function is coupled with an aid function to endow the system with flexibility", not plasticity ([32], p. 471). By contrast, the control functions of living organisms can show plasticity through some self-governing reorganization of their inner wiring, the assumption being that this reorganization will be the basic substrate of functional modifications.

Structural modifications comprise changes in the structural connectivity network (i.e., the connections enabling interactions between elements of a given system) and changes concerning the constitutive elements of the system themselves, of which neurons are the fundamental units. It is now well-accepted that a substantial number of new brain neurons are generated daily. Paillard like others in the field were unaware of adult neurogenesis; indeed, the early evidence from Altman [3] had been effectively ignored. The existence of neurogenesis is poignant to Paillard's comments concerning changes in the elements of a system. This phenomenon occurs in at least two regions of the adult mammalian brain, the subventricular zone and the dentate gyrus (e.g., [1]). However, to understand the functional impact of neurogenesis [21] one also has to take into account several epigenetic cellular factors such as adrenal corticosteroids (e.g., [8]), gonadal hormones (e.g., [40]) and trophic factors (e.g., [11]) as well as physiological and environmental factors like housing conditions, physical exercise (e.g., [19]) and learning opportunities [20]. Furthermore, survival of newly generated neurons may depend on what happens during an initial post-proliferative period of sensitivity, when the newborn cells are in the process of being integrated into cerebral networks [16,41]. From a functional standpoint, the involvement of neurogenesis in memory formation, such as the encoding of time, is one possibility [2,21]. These recent data on adult neurogenesis could not of course have influenced Paillard's views, but his definition of plasticity is nonetheless clearly relevant. For neurogenesis to reach his criterion of plasticity, definitive demonstration is required that newly generated neurones actually contribute to changes in the functional properties of existing networks or systems.

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